

MYCOPHAGY BY *APHAENOGASTER* SPP.
(HYMENOPTERA: FORMICIDAE)

J. F. CARROLL, J. W. KIMBROUGH, AND W. H. WHITCOMB

(JFC) Department of Entomology and Nematology, University of Florida, Gainesville, Florida 32611. Present address: Livestock Insects Laboratory, AEQI, Agric. Res., Sci. and Educ. Admin., USDA, Beltsville, Maryland 20705; (JWK) Department of Botany, University of Florida, Gainesville, Florida 32611; (WHW) Department of Entomology and Nematology, University of Florida, Gainesville, Florida 32611.

Abstract.—The myrmicine ants, *Aphaenogaster ashmeadi* (Emery), *A. floridana* M. R. Smith, *A. miamiana* Wheeler sensu lato, and *A. treatae* Forel, chew fragments from Agaricales basidiocarps and carry the pieces to their nests. Fungi of four genera (*Russula*, *Armillariella*, *Marasmiellus*, *Amanita*) are harvested, but *Russula* basidiocarps are attacked most frequently. Laboratory colonies of four additional species of *Aphaenogaster* have accepted pieces of basidiocarp from a species of *Russula*. *Aphaenogaster* spp. appear to feed on the fungal tissue but may only ingest the fluids. *Aphaenogaster tennesseensis* (Mayr) workers present sporophore fragments to their larvae in the same manner they feed them insect tissue. In our observations ant damage to all basidiocarps except those of *Marasmiellus* is generally less serious than that inflicted by coleopterous and dipterous immatures and adults. These findings may shed new light on the question of the evolution of fungus cultivation by ants. To our knowledge this is the first report of non-attine ants feeding extensively on fungi.

The mycophagous habits of the Attini, or fungus-growing ants, are renowned, but fungus-feeding by ants other than attines is poorly understood. The presence of fungal material in the infrabuccal pockets of ants of several genera (*Pseudomyrmex*, *Crematogaster*, *Lasius*) and fungi growing in the ants' nests led Elliott (1914) to speculate that these ants probably ate fungi. Bailey (1920) and Wheeler (1922) questioned such theories. Bailey believed that the fungal material found in infrabuccal pockets was detritus groomed from nestmates or cleaned from nest galleries. However, Wheeler and Bailey (1920) found that *Pseudomyrmex* larvae were fed the contents of the infrabuccal pockets of workers. They did not determine whether the fungal

material in these food pellets was essential for larval growth. A few ants (*Aphaenogaster*, *Formica*, *Leptothorax*, *Lasius*) were found with bracket fungi, but no feeding was observed (Graves and Graves, 1968; Matthewman and Pielou, 1971). Wellenstein (1952) reported that fungi and carrion constituted 0.3% of the diet of *Formica rufa* L. Using radiotracer techniques, Went et al. (1972) demonstrated that the larvae of *Manica hunteri* (Wheeler) ingested mycorrhizal hyphae that had been growing in a nest of *M. bradleyi* (Wheeler). At least one of two *Megalomyrmex* species that were social parasites of attines ate the symbiotic fungus of its host (Weber 1972).

MATERIALS AND METHODS

Field observations were made in Alachua County in north-central Florida. We examined basidiocarps for the presence of ants. When ants were discovered on a basidiocarp, they were observed for at least five minutes to determine whether they were removing pieces from the fungi. We examined microscopically fungal fragments taken from nestward-bound ants.

Laboratory colonies of eight species of native *Aphaenogaster* (*A. ashmeadi* (Emery), *A. flemingi* M. R. Smith, *A. floridana* M. R. Smith, *A. fulva* Roger, *A. lamellidens* Mayr, *A. miamiana* Wheeler sensu lato, *A. tennesseensis* (Mayr), *A. treatae* Forel) were maintained in standard Wilson nests and in transparent plastic shell vials containing moistened tissue paper. These artificial nests were kept in trays that served as foraging areas for the ants. Laboratory colonies were normally fed hamburger and a variety of dead insects. Fragments of the caps of *Russula* sp., each including spore-laden gills, were offered to all laboratory colonies to determine whether ant workers would carry the fungal tissue into their nests. About 50 workers were removed from an *A. tennesseensis* colony and maintained in a separate artificial nest. For three days the main *A. tennesseensis* colony was given only spore-bearing cap fragments of a *Russula* sp. basidiocarp stained with methyl blue and indocyanine dyes, while the group of 50 was maintained on its regular diet. Staining the fungus enhanced the visibility of fungal fragments in observation nests and made it possible to determine by examination of crop contents whether ants were ingesting fungal material in the form of spores, hyphae, or liquids.

The senior author identified the ants we studied.

RESULTS AND DISCUSSION

We observed four species of *Aphaenogaster* (*A. ashmeadi*, *A. floridana*, *A. miamiana* sensu lato, and *A. treatae*, primarily predators and scavengers) removing fragments from mushroom basidiocarps in the field. Basidiocarps of four genera (three families) were harvested by *Aphaenogaster* spp. Species of *Russula* (Russulaceae) were most frequently harvested.

Additionally, workers of *A. flemingi* were seen visiting a species of *Russula*. *Aphaenogaster ashmeadi* also harvested two species of Tricholomataceae, *Armillariella tabescens* (Scop. ex Fr.) Sing. and *Marasmiellus* sp. Once an *A. miamiana* worker was observed removing a piece from an *Amanita* sp. (Amanitaceae) basidiocarp. To a lesser extent *Pheidole* workers also harvested sporophores. Basidiocarps of several other genera of fungi were available in the foraging areas of the *Aphaenogaster* colonies under observation, but workers were not seen harvesting them. We did not find *Aphaenogaster* workers harvesting conks of bracket fungi, although Graves and Graves (1968) found *A. fulva* workers with Polyporaceae and Thelophora-ceae in North Carolina.

In the field, we observed *Aphaenogaster* spp. harvesting basidiocarps from May to November. The *Marasmiellus* sp. basidiocarps harvested were small (10 mm tall). These sporophores were clipped off near ground level and were removed in single trips by individual *A. ashmeadi* workers. An *A. ashmeadi* worker would straddle the stipe of a felled *Marasmiellus*, grip it just below the cap with her mandibles, and carry it nestward. *Marasmiellus* basidiocarps taken from foraging ants were slightly immature. Only in the case of *Marasmiellus* did ants apparently damage basidiocarps before spores matured. Large (6 cm tall, 6 cm diam cap) and medium-sized basidiocarps, such as those of some *Russula* spp., never appeared to be entirely removed by ants. *Aphaenogaster* spp. chiefly attacked the caps of *Russula* spp., particularly along the rims. Chunks of basidiocarp tissue up to about 3 mm³ were chewed off by individual *Aphaenogaster* workers and were carried nestward. *Aphaenogaster ashmeadi* took pieces from caps and stipes of *Armillariella tabescens*. One clump of *Ar. tabescens* was harvested by *A. ashmeadi* workers for eight days. During 1 hr in the afternoon 20 *A. ashmeadi* workers carried pieces (most about 2 mm³) of *Ar. tabescens* to their nest. As many as eight *Aphaenogaster* spp. workers were seen simultaneously visiting individual *Russula* basidiocarps. Most basidiocarps harvested were mature or senescent. Individual *Russula* sp. were usually attacked for two to five days by *Aphaenogaster* spp. However, they eventually decayed or were eaten by organisms other than ants. The effect of ant harvesting on spore mortality or dissemination (and thus on the fitness of the fungal organisms) remains to be assessed.

In the laboratory, workers of *A. ashmeadi*, *A. flemingi*, *A. floridana*, *A. fulva*, *A. lamellidens*, *A. miamiana*, *A. tennesseensis*, and *A. treatae* carried pieces of *Russula* into their nests. We observed that basidiocarp fragments carried into artificial nests by foragers were subsequently torn to pieces by the ant workers. One to three ants chewed a fragment. At times *A. tennesseensis* workers held fungal fragments with their mandibles; rather than chewing the fungal tissue, they appeared to imbibe fluid from it. Workers placed larvae on some fungal fragments, and very small fragments were

placed on the upturned venters of larger larvae. The anteriors of the larvae extended in characteristic feeding position. Buschinger (1973) and others have described such larval feeding behavior in *Aphaenogaster* colonies given insects as food. Eventually the ants discarded the masticated tissue within and outside their nests.

Microscopic examination of fungal fragments taken from nestward-bound workers revealed no minute invertebrates, although most sporophores damaged by ants contained coleopterous or dipterous immatures or adults. Crop contents of workers examined before they were given dyed basidiocarp tissue were yellowish-brown, as were those of five workers from the group of 50 *A. tennesseensis* given hamburger during the three day period. Crop contents from 17 of 18 workers from the *A. tennesseensis* colony given dyed pieces of *Russula* daily for three days were blue-green like the dye. *Russula* spores were found in the crop of only one of 18 workers from the *A. tennesseensis* colony given dyed basidiocarp fragments. Some of these workers were collected directly from pieces of fungi on which they were chewing. The absence of spores in the crops containing dye suggested that workers ingested mostly fluids from the fungal tissue. Microscopic examination of the contents of the infrabuccal pockets from ten *A. tennesseensis* workers with blue crop contents showed no spores or hyphae. Whether the ants regurgitated the fungal material from their infrabuccal pockets or it was digested was not shown by these results. However, spores are generally digestible only in solutions of extreme pH and *Russula* spores are small (often $< 10 \mu$ diam), reducing the likelihood they are filtered out before they can reach the crop. By comparison Eisner and Happ (1962) have found that corundum particles as large as 100μ diam pass into the crops of workers of the somewhat larger *Camponotus pennsylvanicus* (DeGeer).

Fungal tissue may be more than merely a source of moisture for *Aphaenogaster* spp. Workers drank from moistened balls of tissue paper placed in their foraging areas. Moistened balls of tissue paper were placed in foraging areas of an *A. tennesseensis* colony and an *A. ashmeadi* colony simultaneously with fungal fragments of similar size. About five times as many ants were attracted to the fungal fragments as to the wet tissue paper.

Any nutritive importance of basidiocarps to *Aphaenogaster* spp. remains to be assessed. The symbiotic fungi of the Attini apparently provided those ants their essential nutrients (Weber, 1972). None of the *Aphaenogaster* spp. observed were found tending Homoptera or visiting extrafloral nectaries—important carbohydrate sources for many ants. In the laboratory, however, when *Aphaenogaster* spp. colonies were presented balls of tissue paper soaked with water and other tissue balls soaked with sugar water, the ants swarmed on the balls with sugar water and virtually neglected tissue moistened with plain water. Van Pelt (1958) found *Aphaenogaster* spp. attracted to molasses, and Carroll (1975) found *A. miamiana* visiting sap

exuding from an elm, *Ulmus* sp. We do not know if Agaricales sporophores serve primarily as a carbohydrate source for *Aphaenogaster* spp.

On three occasions we found *Pheidole dentata* Mayr workers harvesting a species of *Russula*, and once we saw a *P. metallescens* Emery worker removing a piece of *Russula* basidiocarp. *P. dentata* workers were twice observed harvesting *Amanita* sp., and one *P. dentata* worker was found carrying some basidiocarp of *Marasmiellus*. We saw no other ants harvest basidiocarps, and the significance of mycophagy in the competition between *Aphaenogaster* spp. and other terrestrially foraging ants was not clarified.

These findings may aid in understanding the evolution of the fungus-growing attines. Several explanations of the phenomenon have been propounded. Attines, according to von Ihering (1894), could have evolved from harvesting ants that ate mold growing on their stored seeds. Goetsch and Gruger (1942) reprised von Ihering's basic hypothesis. Emery (1899) held that cropping of adventitious hyphae on the walls of ant nests by the inhabitants was probably the origin of mycophagy in ants. Forel (1902) felt that proto-attines nested in rotten wood and consumed fungi growing on feces of wood-boring insects. More recently, Weber (1956, 1972) suggested that proto-attines could have begun feeding on fungi growing on the ants' own feces. In 1946 Wolcott observed some workers of the attine *Acromyrmex coronatus* (Fabricius) "eating," i.e., cutting up and removing basidiocarps of *Pleurotus* sp. in the manner we have described for *Aphaenogaster*. He referred to such behavior as "recessive traits," i.e., a reversion from the agricultural state. Wojcik (personal communication) discovered *Cyphomyrmex rimosus* (Spinola) similarly harvesting an unidentified basidiocarp, and the senior author observed *Trachymyrmex septentrionalis* (McCook) workers removing pieces of a *Russula* sp. basidiocarp. Both ants were attines.

We do not wish to imply that attines have evolved from *Aphaenogaster*, but we do suggest that a generalized myrmicine ant with *Aphaenogaster*-like or, perhaps, *Pheidole*-like habits is a plausible ancestor. However, von Ihering (1894) has cited *Aphaenogaster* as one of the genera of seed-harvesters having habits like those of his postulated attine precursor. Perhaps the feeding behavior of the proto-attine resembled that of present day *Aphaenogaster* spp., which Smith (1961) and Buschinger (1973) have described as generalized and in some aspects primitive members of the Myrmicinae. The proto-attines may have carried spore-laden fungal fragments to their nests and, after macerating the fungal tissue, may have discarded it in refuse areas in their nests. Refuse areas of omnivorous ants such as *Aphaenogaster* spp., which also collect seeds (Culver and Beattie, 1978) and floral parts of plants, contain a variety of substrates on which fungi may flourish in humid nest conditions. Such conditions may have favored co-evolution of a symbiosis between the ants and fungi.

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